


The effects of the invasive species, *Lantana camara*, on regeneration of an African rainforest

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Abstract

Invasive plants adversely affect native communities by altering ecosystem function and disrupting natural regeneration. We investigate the effect of invasive *Lantana camara* L. (Verbenaceae) on forest regeneration in Kibale National Park, Uganda. We appraise the efficacy of cutting and uprooting *Lantana* for promoting native tree recruitment. Sample plots comprised three types: (i) currently invaded by *Lantana*; (ii) cleared of *Lantana* and now managed; and (iii) forest reference plots uninvaded by *Lantana*. Tree species numbering 51, 19 shrubs, and 17 herb species were identified. *Lantana* reduced tree, shrub, and herb cover and diversity, and suppressed tree regeneration. The short-term management of *Lantana* did not promote tree establishment. The tree community in cleared areas was not converging on uninvaded adjacent forest. *Lantana* is known to allelopathically suppress tree seedling establishment, but even at sites cleared of *Lantana*, tree species recruitment was poor. While insufficient time may have passed for tree recruitment, we argue that an increase in shrub and herb cover and diversity arrested forest tree regeneration. Sustained follow-up clearing of dense secondary shrubs and herbs and resprouted *L. camara* in cleared areas is key to ensuring long-term recovery of the forest tree community.

KEYWORDS

carbon-offset projects, forest regeneration, invasive alien species, restoration ecology, tropical forest management

Résumé

Les plantes envahissantes nuisent aux communautés indigènes en modifiant la fonction des écosystèmes et en perturbant la régénération naturelle. Nous étudions les effets de l'envahissant *Lantana camara* L. (Verbenaceae) sur la régénération de la forêt dans le parc national de Kibale, en Ouganda. Nous évaluons l'efficacité de la coupe et du déracinement du *Lantana* pour promouvoir le recrutement d'arbres indigènes. Les parcelles d'échantillonnage étaient de trois types: (i) actuellement envahies par le *Lantana*; (ii) débarrassées du *Lantana* et maintenant gérées; et (iii) parcelles de référence

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forestières non envahies par le *Lantana*. 51 espèces d'arbres, 19 arbustes et 17 espèces d'herbes ont été identifiés. Le *Lantana* a réduit la couverture et la diversité des arbres, des arbustes et des herbes, et a supprimé la régénération des arbres. La gestion à court terme du *Lantana* n'a pas favorisé l'établissement des arbres. La communauté d'arbres dans les zones défrichées ne convergeait pas vers la forêt adjacente non défrichée. Le *Lantana* est connu pour supprimer de manière allélopathique l'établissement des semis d'arbres, mais même sur les sites débarrassés du *Lantana*, le recrutement des espèces d'arbres était faible. Bien que le temps ait pu être insuffisant pour le recrutement des arbres, nous soutenons qu'une augmentation de la couverture et de la diversité des arbustes et des herbes a arrêté la régénération des arbres de la forêt. Un suivi régulier du défrichage des arbustes et des herbes secondaires denses et de la repousse du *L. camara* dans les zones défrichées est essentiel pour assurer le rétablissement à long terme de la communauté d'arbres de la forêt.

1 | INTRODUCTION

Tropical rainforests cover approximately 7% of the earth's surface, but harbour close to half of the world's plant species and support high levels of biodiversity (Eiserhardt et al., 2017). Furthermore, tropical forests and wetlands could contribute 23% of the mitigation needed to stabilise global warming below 2°C by 2030 (Griscom et al., 2017; Wolosin & Harris, 2018). However, ~60 million ha of tropical forest, equivalent to the area of Madagascar, were lost from 2002 to 2019 (Weisse & Gladman, 2020). As forests in the tropics continue to undergo rapid conversion to agricultural and pastoral lands, it is becoming increasingly clear that the survival of many forest species will depend on the capacity of disturbed forests to be restored and support plant and animal populations (Chapman et al., 2018; Omeja et al., 2016).

While rainforests can regenerate successfully after disturbances, recovery pathways can also deviate from the pre-disturbance state (Chapman et al., 1999; Romero et al., 2013). Invasive plant species can disrupt recovery pathways by altering species interactions and ecosystem structure and functioning (Webster et al., 2018; Zhang et al., 2014). *Lantana camara* L., Sp. Pl. [Linnaeus] (1753) (hereafter *Lantana*) is a significant invasive plant (Goncalves et al., 2014) with a global distribution of approximately 60 countries or island groups between 35°N and 35°S, outside its native range in Central America, northern South America and the Caribbean. It has allelopathic properties that inhibit the growth of other species growing close to it (Sharma et al., 2005), its dense growth form suppresses seedling regeneration and limits disperser movement (Prasad, 2012), and it increases fire risk (Berry et al., 2011). Where *Lantana* persists, it can lead to significant changes in the structure and floristic composition of natural communities and reduce biodiversity (Gooden et al., 2009; Sundaram & Hiremath, 2012). For example, in Bandipur Tiger Reserve, India, vast areas of impenetrable *Lantana* thickets prevent access by herbivores to foraging areas (Prasad, 2007), affecting habitat structure and dynamics. Environmental changes associated

with invasive weed species include a reduction in resource availability, forcing wildlife to seek food outside protected area boundaries, so increasing human-wildlife conflicts (Hartter et al., 2012), but also a reduction in the ecological resilience of natural habitats, making them vulnerable to changing climate (IUCN, 2017). Numerous control or eradication methods have proved largely unsuccessful, including mechanical removal and biological control (Bhagwat et al., 2012; Love et al., 2009), although some chemical methods show promise (Somerville et al., 2011).

At Kibale National Park in western Uganda, a programme of restoration tree planting has been ongoing since the mid-1990s with the aim of re-establishing forest stands at previously disturbed sites (commercial forestry; agricultural pasture/grassland) with high tree species density and diversity, and forest wildlife in general (Nyafwono et al., 2015). However, the progress of reestablishment of forest trees is often slowed or arrested by fast-growing shrub species, vines, ferns, or grasses (Duncan & Chapman, 2003a, 2003b). In addition, disturbed areas subject to restoration tree plantings are ideally predisposed to invasion by native woody herbs (e.g., *Acanthus pubescens* Engl., Lawes & Chapman, 2006) and invasive species such as *Lantana* (Owiny, 2016). *Lantana* is a rapidly establishing invasive species and is widespread at many uncleared disturbed sites, as well as at cleared sites in Kibale National Park (Omeja et al., 2011, 2016), where dense thickets suppress the regeneration of native woody species.

We assessed plant diversity and forest physiognomy in areas of semi-deciduous regenerating rainforest in Kibale National Park. We compared established rainforest tree diversity with the recovery trajectory of tree diversity in cleared areas invaded by *Lantana*. *Lantana* invasion was managed by cutting the main stems at their base or uprooting the plant where possible. We address if (1) *Lantana* has a suppressive effect on the regeneration of native woody species, and based on our findings, we (2) recommend effective methods of rehabilitating and restoring previously actively managed (logged) forest stands that have been invaded by *Lantana*.

2 | METHODS

2.1 | Study area

The study was conducted in Kibale National Park (hereafter Kibale; 795 km²), which is 24 km east of the Rwenzori Mountains and 20 km south-east of the town of Fort Portal in western Uganda (Figure 1). The park ranges in altitude from 1590 m in the north to 1110 m in the south and its annual rainfall averages 1671 mm (1970–2021, Chapman C.A. unpublished data) falling in two rainy seasons (March – May; September – October). The forest cover is broadly classified as moist evergreen in the north and moist semi-deciduous in the south.

The area that is now Kibale has experienced several human-induced disturbances in the last century (Chapman et al., 2005, 2010). The area became a national park in 1993, prior to this it was a forest and game reserve that was established between 1926 and 1932 (Chapman & Lambert, 2000; Struhsaker, 1997). In the early 1970s, illegal destruction and encroachment by subsistence farmers occurred in the south, but in 1992 the encroaching populations were resettled away from the park under a UN resettlement programme.

The most reliable estimate of the number of people residing in the southern corridor is 8800 (van Orsdol, 1986).

The study area is regenerating forest in the southern section near Mainaro (Figure 1) that had once been disturbed by subsistence agriculture, but has since been protected from fire and subjected to enrichment planting as part of a carbon-offset programme (Face, 2011; Wheeler et al., 2016).

Forest restoration commenced in 1994 under the joint efforts of the Uganda Wildlife Authority (UWA) and Face the Future (previously Forests Absorbing Carbon Emissions (FACE Foundation) (Omeja et al., 2011, 2012; Wheeler et al., 2016)). Restoration involved fire protection and the planting of millions of seedlings that were raised from seeds or collected from the wild. Vegetative propagation by cuttings accounted for 5% of the trees planted. Seedlings were planted along 2-m wide paths, with each seedling planted in the centre of a 5 m × 5 m cell, yielding 400 tree seedlings per hectare. After planting, the seedlings were monitored and weeded two to three times a year for the first few years.

These abandoned agricultural lands are ideally suited to invasion by native woody herbs, such as *Acanthus pubescens* Engl. and *Mimulopsis* spp., shrubs such as the invasive shrub-thicket species, *L. camara*, and the grass *Pennisetum purpureum* Schumach., that slow forest recovery (Duncan & Chapman, 2003a; Lawes & Chapman, 2006). Of these species, the invasive *L. camara*, stands out because it had become the dominant understory species invading large areas where the restoration efforts took place. To promote forest regeneration, UWA started cutting and uprooting *Lantana* in December 2016 and by February 2017, 80.4 ha were cleared.

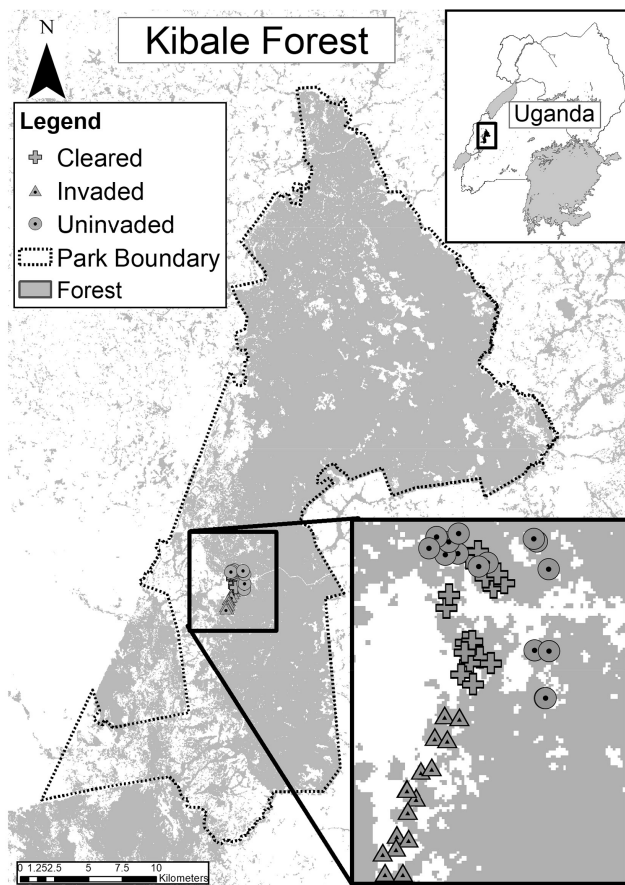


FIGURE 1 Map of study location and sample sites categorised by their *Lantana* management status as cleared, invaded and uninvaded. The sample plots are located in the Mainaro region of Kibale National Park.

2.2 | Study design

Three plot categories were identified in the replanted areas based on *Lantana* invasion intensity and management history: (i) *Lantana* invaded sites comprising $\geq 50\%$ *Lantana* cover with no history of *Lantana* removal; (ii) reference sites comprising intact native vegetation with $\leq 5\%$ *Lantana* cover; and (iii) cleared sites where *Lantana* had been removed. Paired edge and interior 5 m × 5 m plots were established in each of the three plot categories with edge plots located close to forest trails and interior plots placed in undisturbed forest ≥ 100 m from and perpendicular to the forest trail edge plot (Figure 2). Forest trail edge conditions were selected because *Lantana* is considered a light-dependent, forest-edge species (Prasad, 2012) that grows particularly well in unshaded and disturbed habitat (Sharma et al., 2005; Wilson et al., 2013). The interior closed-canopy forest was not expected to be invaded by *Lantana* because of the low light conditions (Prasad, 2012). Within each plot category, eight paired plots were laid out at intervals of ≥ 100 m between the pairs. Using this design, our study comprised two treatments and two controls; the treatments included forest edge areas that are (i) currently invaded by *Lantana* and (ii) previously invaded but now cleared, whereas the controls were (i) intact forest trail edges and (ii) the forest interior. The forest edge plots were sited in areas with open

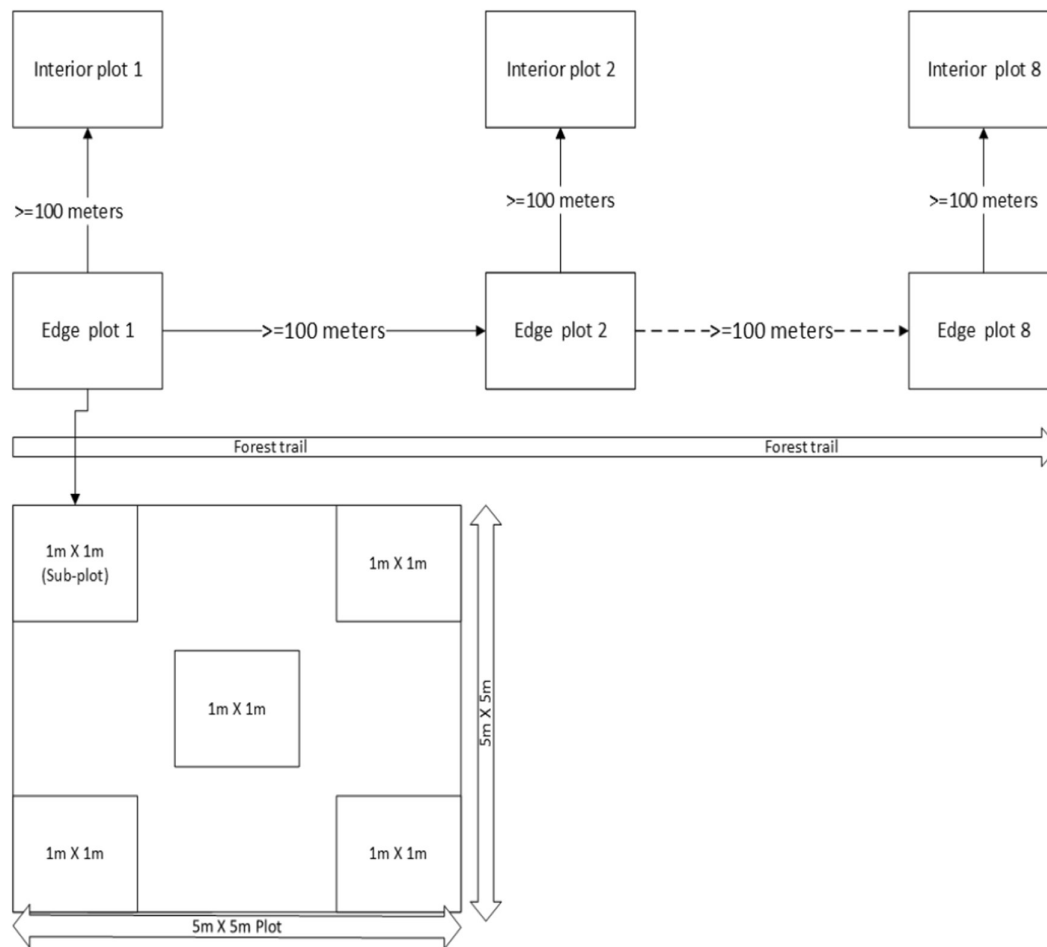


FIGURE 2 Design of plot and sub-plot layout used to assess the effects of *Lantana* and its removal on forest regeneration in Kibale National Park, Uganda.

canopy cover ($\leq 50\%$) and the forest interior plots under closed canopy cover ($\geq 70\%$).

Trees were sampled in $5\text{ m} \times 5\text{ m}$ plots, which are an appropriate size for examining interactions among small trees and shrubs (Duncan & Chapman, 2003b). Shrub and herb cover in the $5\text{ m} \times 5\text{ m}$ plots were sub-sampled in five $1\text{ m} \times 1\text{ m}$ sub-plots that were arranged in each of the four corners and one at the centre of the larger plot (Figure 2). Shrubs and herbs were assessed in $1\text{ m} \times 1\text{ m}$ sub-plots because of their abundance and the difficulty of assessing their cover over the whole $5\text{ m} \times 5\text{ m}$ area. Eight paired plots were established in each invasion category giving a total of 16 plots and 80 sub-plots for each category and a total of 48 plots and 240 sub-plots.

2.3 | Vegetation assessment

Three vegetation growth forms were assessed; trees, shrubs, and herbs. Small trees were enumerated in three diameter size classes: 5–10 cm (measured at 130 cm), 2–5 cm (with height above 150 cm – measured at 50 cm), and tree seedlings ($\leq 2\text{ cm}$ measured at the root collar). Trees with diameter $> 10\text{ cm}$ were not counted as these were

considered part of the advanced regeneration predating *Lantana* invasion. Foliage percent cover was visually estimated for shrubs and herbs as a proportion of sub-plot area. Plants were identified in the field using the plant field guides in Hamilton (1991) and Katende et al. (1995). Plants that could not be identified in the field were assigned a unique label and voucher specimens were taken to the Makerere University Herbarium for identification.

2.4 | Data analysis

Of the 24 forest interior or intact plots, nine had $>5\%$ *Lantana* and were omitted from the analysis. Of the remaining 15 forest interior plots (reference plots), eight were randomly selected for comparison with the eight plots in each *Lantana* invasion category. Two-way analysis of variance (invasion category by diameter size class) was used to assess the differences in tree species density (individuals per plot), tree and herb/shrub density and richness among *Lantana* invasion categories. Comparison of means was by Tukey's test.

Species diversity and richness were compared among the invasion categories using Hill's diversity numbers (Hill, 1973). Hill's

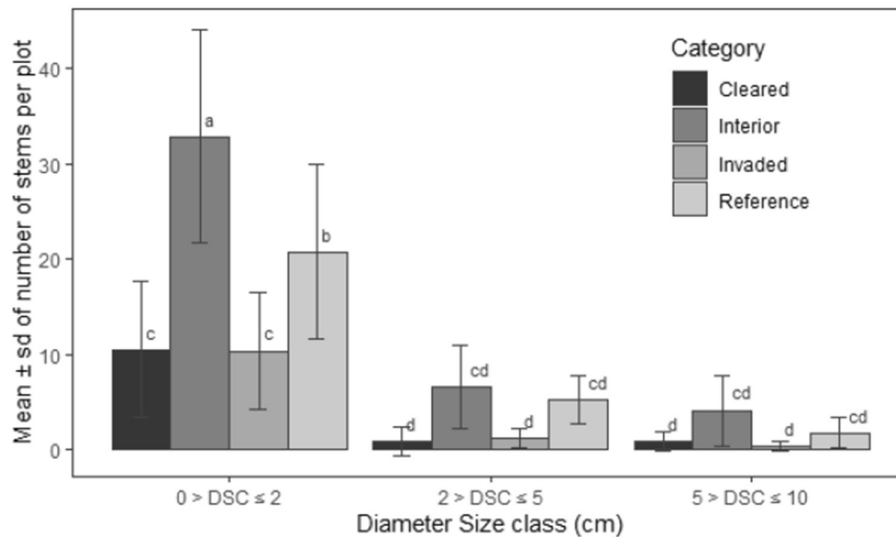


FIGURE 3 Tree density diameter distribution by diameter size class in the *Lantana camara* invasion management categories in Kibale National Park, Uganda. Letter labels above bars indicate significant differences (Tukey's test) in the diameter size class means among the invasion categories. Reference sites are in adjacent forest interior not yet invaded by *Lantana*.

TABLE 1 Results for one-way analyses of similarity (R – value in ANOSIM) pairwise comparisons of tree species composition between the *L. camara* invasion management categories ($n = 8$ plots in each category).

Treatments	Cleared	Invaded	Uninvaded/reference
<i>p</i> -Value			
Interior	0.001***	0.011**	0.017**
Cleared		0.134	0.001***
Invaded			0.003***
<i>R</i> -value			
Interior	0.248	0.204	0.184
Cleared		0.074	0.564
Invaded			0.393

Note: ANOSIM were undertaken for all tree species (presence/absence) among *L. camara* cleared, invaded, uninvaded reference and forest interior sites. Uninvaded or reference plots were located in adjacent forest interior sites that were not yet invaded by *Lantana*. Asterisks denotes statistical significance with ** $p < 0.01$ and *** $p < 0.001$.

diversity numbers (Ludwig et al., 1988) are easier to interpret than many other diversity indices (Magurran, 1988) and are relatively unaffected by species richness and independent of sample size (Ludwig et al., 1988). Simpson's (D_s) and Shannon-Wiener (H') indices of diversity were used in the derivation of the Hill's numbers. From Hill's family of diversity numbers, N_1 (number of abundant species) and N_2 (number of very abundant species) were selected as measures of species diversity; N_0 measures species richness, and species evenness was estimated using the E5 index (Ludwig et al., 1988).

To determine the recovery pathway after *Lantana* clearing and if it is converging on forest conditions, only tree species in the 2–5 cm dbh size class were used. This diameter size class represents the

regeneration most likely to have been recruited since management intervention (i.e., 2 years of growth) and that will survive to mature trees (Piiroinen et al., 2017). Smaller and larger diameter size classes are less indicative of successful recruitment under *Lantana* conditions, because they either experience high mortality or were present prior to *Lantana* invasion, respectively.

Tree species composition among invasion categories was compared using one-way analysis of similarity (ANOSIM) and similarity percentage analysis (SIMPER), computed using Community Analysis Package (CAP) version 4.1.3 (Henderson & Seaby, 2007). These analyses compared the similarity of species composition among *Lantana* invasion categories and the within-group similarities and dissimilarities among the *Lantana* invasion categories, respectively. Analyses were based on presence/absence data of tree species. Estimates of compositional similarity among *Lantana* invasion categories were determined using the Bray–Curtis similarity matrix (Clarke, 1993). The mean percent cover of shrubs and herbs was visually estimated from the five sub-plots in each plot.

3 | RESULTS

Tree stem density varied significantly among invasion categories ($F_{3,84} = 21.1$, $p < 0.0001$; Figure 3) and within stem diameter size classes among invasion categories ($F_{6,84} = 6.9$, $p < 0.0001$; Figure 3). The plots that were not invaded by *Lantana* (uninvaded and interior plots) displayed higher tree densities than the invaded and cleared plots (Table S1). The smallest trees (≤ 2 cm dbh) contributed most to stem density across all the *Lantana* invasion management categories comprising 69.2% of the total density. This was followed by trees between 2 and 5 cm dbh that accounted for 20.7%, while the biggest trees (5–10 cm) had the lowest density at 10.2% (Figure 2).

Computed indices		<i>L. camara</i> invasion management categories			
		Interior	Invaded	Cleared	Reference or uninvaded
Diversity indices	N1	29.7	16.3	16.0	24.9
	N2	33.3	19.3	17.8	30.2
Richness index	N0	37	20	21	33
Evenness index	E5	1.13	1.19	1.12	1.22

TABLE 2 Summary of diversity indices computed for *L. camara* invasion management categories.

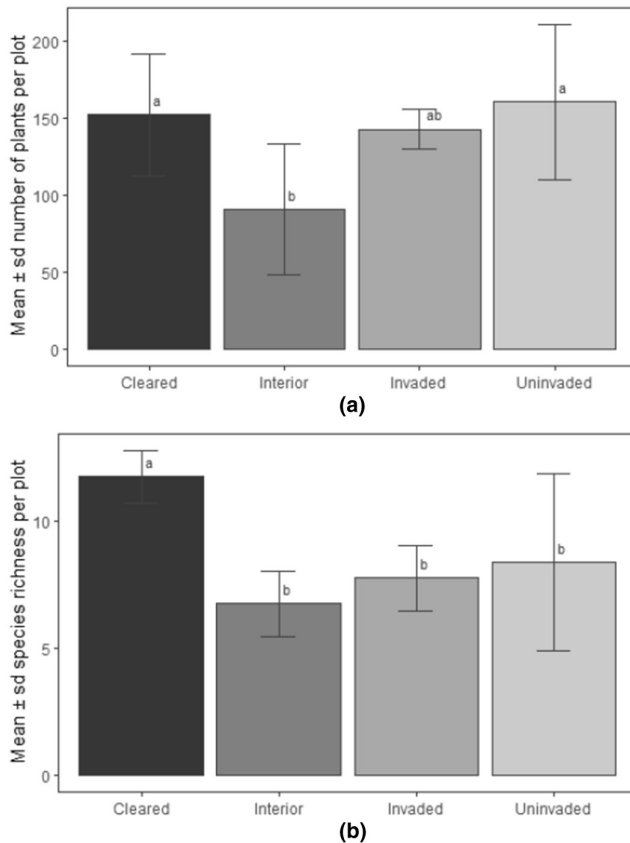


FIGURE 4 Shrub and herb abundance (a) and species richness (b) among the *Lantana* invasion categories defined in this study. Letter labels above bars indicate significant differences (Tukey's test) in the diameter size class means among the invasion categories. Reference sites (interior) are in adjacent forest interior not yet invaded by *Lantana*.

Fifty-one tree species were recorded in the plots (Table S1). Tree species composition differed significantly between interior plots and all plots in other invasion categories (Table 1). Sites invaded by *Lantana* and from which *Lantana* was cleared displayed similar tree composition (Table 1). The most abundant tree species in the invaded plots was *Albizia grandibracteata* Taub. (Fabaceae), while *Bridelia micrantha* (Hochst.) Baill. (Euphorbiaceae) was most abundant in the plots that were cleared of *Lantana*, and *Funtumia africana* (Benth.) Stapf (Apocynaceae) was abundant in both the uninvaded forest trail edges and forest interior plots. Tree species richness (N0) differed among plot types with the most species recorded in plots not invaded by *Lantana* (interior plots 37; uninvaded forest trail edges 33;

TABLE 3 ANOSIM (*R*-value) pairwise comparisons of shrub and herb species composition between the *L. camara* invasion management categories.

Treatments	Cleared	Invaded	Uninvaded/reference
<i>p</i> -Value			
Interior	0.002***	0.001***	0.14
Cleared		0.001***	0.002***
Invaded			0.001***
<i>R</i> -value			
Interior	0.509	0.906	0.093
Cleared		0.572	0.335
Invaded			0.931

Note: ANOSIM were undertaken for all shrubs and herbs species (percentage data) among *L. camara* managed, invaded, uninvaded reference and forest interior sites. Asterisks denotes statistical significance with *** $p < 0.001$.

cleared 21, invaded 20). The number of abundant species (N1) was greatest in interior plots (29.7), then uninvaded (24.9) and invaded (16.3), and least in the cleared plots (16.0; Table 1). The number of very abundant species (N2) was greatest in interior plots (33.3), then the uninvaded areas (30.2) and invaded (19.3) and cleared areas (17.8) (Table 2). The forest interior and managed (cleared of *Lantana*) plots had a marginally more even distribution of species (E5) than the uninvaded plots and invaded plots (Table 2). Size class stem frequency distributions followed the expected reverse J-shape with continuous regeneration and a general decline in stem density with increasing diameter size class.

Nineteen shrub and 17 herb species were identified (Table S2). Shrub and herb cover varied among invasion categories ($F_{5,28} = 5.09$, $p < 0.006$), with greater cover in plots at disturbed sites (cleared of, invaded and uninvaded by *Lantana*) than in the forest interior (Figure 4a). In disturbed areas, shrub and herb species richness in plots that were cleared of *Lantana* was significantly greater than in any other invasion category, which displayed similar species richness (Figure 4b). *Lantana* invasion appeared to suppress shrub and herb diversity, evidenced by the lowest species richness in the invaded areas (17) and the highest species richness in cleared areas (29). The forest interior and uninvaded areas had more similar shrub and herb species richness (20) (Table 3).

The shrub and herb species composition differed among plot types (ANOSIM $R = 0.589$, $p < 0.001$), with five of six pair-wise comparisons being significantly different. Only the uninvaded and forest

interior plots did not differ (Table 3, $R = 0.093$, $p = 0.14$). SIMPER similarity within the *Lantana* invasion management categories was greatest in the invaded areas. Shrub and herb evenness were observed in invaded plots, while the cleared plots were most heterogeneous in composition.

4 | DISCUSSION

Trees were most dense in uninvaded reforested areas, and least dense in areas that were previously and currently invaded by *Lantana*. The low density of the small size classes in invaded areas could be due to *Lantana* limiting seedling recruitment by competing for light, nutrients and space, as well as putative allelopathic effects (Gooden et al., 2009; Lambert et al., 2017; Prasad, 2012; Shackleton et al., 2017). The present study confirms the general suppressive effect of *Lantana* invasion on biodiversity and ecosystem functioning (Dobhal et al., 2011; Omeja et al., 2011; Ruwanza, 2020). Cutting and uprooting *Lantana* at Kibale did not lead to expected recovery of native tree density, species diversity, richness, and evenness in the reforested plots. Tree density did not vary significantly between invaded areas where *Lantana* had been removed by the Uganda Wildlife Authority and those without management, suggesting that available microsites for saplings were saturated in all categories. The lower richness and diversity and greater evenness of sapling species at cleared and invaded sites, observed also in other studies (Jevon & Shackleton, 2015; Ruwanza, 2020), may reflect the long-lasting effect of the allelopathy of *Lantana* at managed sites, or simply that many tree species have not had sufficient time since management to disperse into the plots, establish, and grow. This suggests that the removal of *Lantana* without follow-up management will not necessarily facilitate tree recovery in the reforested areas. While further monitoring is required to confirm the latter, a removal experiment measuring the effect of bridal creeper (*Asparagus asparagoides* (L.) Druce) concluded that more than 8 years of monitoring is needed to assess if similar weed control was successful (Turner & Virtue, 2006).

The tree species size – frequency distribution patterns provide some hope that continued management will be successful. Across all *Lantana* invasion management categories, a reverse J-shaped distribution pattern of tree sizes was observed, indicating continuous tree species regeneration as required for forest recovery. However, only 24 of 51 tree species were found in the diameter size class (2–5 cm), which represents the advanced regeneration most likely to survive to mature trees. Only five of these (*Funtumia africana* (Benth.) Stapf, *Celtis gomphophylla* Baker, *Antidesima membranaceum* Müll. Arg., *Diospyros abyssinica* (Hiern) F. White and *Euadenia eminens* Hook. f.) were also present in smaller diameter size classes. These five species were also among the most abundant species across all treatments. Twenty-four of the remaining 27 species that were absent in the larger diameter size classes were present only in the seedling diameter size class, suggesting that there is the potential for a more diverse regeneration community in the future.

The species composition of five of the six ANOSIM pairwise comparisons of tree species composition differed, with only cleared and invaded areas being similar. Cleared and invaded areas may be more similar either because of persistent effects of *Lantana* on the ecosystem (e.g., allelopathic effects) or because of limited tree regeneration due to increased non-tree species cover in these areas. The invaded areas were dominated by thickets of *Lantana*, while the areas where *Lantana* had been removed had dense secondary invasion that can also limit tree regeneration through increased competition for resources (Duncan & Chapman, 2003b; Lawes & Chapman, 2006). The largest tree composition dissimilarity was between invaded areas and the uninvaded reforested areas (see also Gooden et al., 2009 for similar results in a wet sclerophyll forest in Australia). Only two species, *F. africana* and *A. membranaceum*, were common to both cleared and uninvaded areas.

The management of *Lantana* was associated with increased shrub and herb cover and diversity relative to the forest interior plots as has also been observed in Australia (Gooden et al., 2009) and India (Prasad, 2012). This may have been driven by the reduction in the *Lantana* and its influence, increased propagule supply after clearing and by the soil disturbance created by the weed management itself (Yeates & Schooler, 2011). Removing *Lantana* releases shrubs and herbs from resource competition and with more resources available, opportunistic herbaceous and woody colonisers thrive (Gooden et al., 2009), and secondary weed invasion may occur. The uninvaded edge areas had similarly high herb/shrub coverage compared to the invaded and cleared areas, suggesting *Lantana* management fosters dense secondary invasion by shrubs and herbs. These herbs and shrubs clearly further arrest tree succession by their competitive dominance that hinders tree recruits, slowing the forest recovery process (Lawes & Chapman, 2006).

Attempts to eradicate *Lantana* date back to at least 1921 in India (Troup, 1921) and substantial management efforts were well under way in the 1970s in both South Africa and Australia (Bhagwat et al., 2012). Australian efforts concentrated on bio-control, in South Africa control methods focused on mechanical removal, while in India control included these methods as well as chemical control (Babu et al., 2009; Bhagwat et al., 2012; Love et al., 2009; Priyanka & Joshi, 2013). These methods were selected to halt or slow the rapid rate of invasion and the costs, both economic and ecological, that *Lantana* inflicted on the ecosystems they invaded (Goncalves et al., 2014). For example, by the early 1980s *Lantana* had invaded approximately 2.2 million ha in South Africa, nearly 2% of the land area, and neither mechanical nor chemical control had proven effective at eradication (Cilliers, 1983). In Queensland, Australia, the cost of *Lantana* invasion to the grazing industry was estimated at US\$121 mil. in 2007, which is equivalent to US\$162 mil. today (Bhagwat et al., 2012). In the area of southern Uganda that supports approximately 90% of the country's cattle population, surveys suggest that *Lantana* costs individual households US\$400–500 per year (Shackleton et al., 2017). In a country where the typical annual salary is only about \$7000 USD, this is a substantial perceived cost. Despite the

importance of managing *Lantana's* spread and the efforts made globally, but particularly in Australia, South Africa, and India, all eradication methods have been largely unsuccessful (Bhagwat et al., 2012; Priyanka & Joshi, 2013). Studies such as the present one are necessary to determine the recovery potential of forest under *Lantana* management.

Mechanical removal of *Lantana* in Kibale, while requiring further long-term monitoring and trials that control weed invasion following *Lantana* removal, does not look promising. Elsewhere, low-volume high-dose applications of glyphosate, an ecologically harmful herbicide, have proved successful for *lantana* control using the splatter gun approach (Somerville et al., 2011). We argue that rather than attempting to entirely eradicate *Lantana*, it should be managed to minimise its impact by applying methods that are easy to apply and inexpensive. Top killing *Lantana* by cutting at or below the root collar and then removing the residue for fuel production is one such approach. Removing resprouted *Lantana* stems in subsequent management follow-up should eventually exhaust root reserves and lead to the death of individual *Lantana* plants, as has been applied to the similarly thicket-forming *Chromolaena odorata* (L.) R.M.King & H.Rob. (Ramaano et al., 2021). Removal of new *Lantana* recruits before they reproduce is critical to the success of this mechanical control method. This study shows that such management can progress forest tree recovery. Lastly, *Lantana* is already being used as a fuelwood source in India (Sharma & Raghubanshi, 2007) and Ethiopia (Bahru et al., 2021) as it has suitable levels of heat production (Kumar et al., 2009). Thus, *Lantana* harvesting and potential briquette making that involve local community members warrant further consideration and study.

AUTHOR CONTRIBUTION

AB, CC, PO, ML designed the study. AB conducted the field work with the assistance of PO. AB and ML conducted the analysis. MN helped with taxonomic identification. AB, ML, CC wrote the manuscript. All co-authors commented on and approved the final version of this article.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest in relation to this study.

DATA AVAILABILITY STATEMENT

Summaries of the data are available in the supplementary data and the full dataset is available on request from either AB or ML.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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